PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(2):341–355. 2003.

Skull osteology of the characid fish *Astyanax mexicanus* (Teleostei: Characidae)

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Abstract.—The skull of the characid fish *Astyanax mexicanus* is described based on twenty alizarin-stained adult specimens from Río Salado, Río Conchos, Río Alamo, and Río San Juan populations, all of them Rio Grande tributaries in Northeastern Mexico. The skull has a circular shape in lateral view. The second infraorbital is triangular and never overlaps the inferior margin of the third infraorbital. The third infraorbital never reaches the laterosensory canal of the preopercular bone. The supraoccipital is short. The palatines, ectopterygoids and mesopterygoids lack teeth. We describe two features not reported in *Astyanax* before: teeth on the second suspensory pharyngeal and posterior gill rakers on the four gill arches. Differences in skull osteology between *A. mexicanus* and other described species of *Astyanax* are denoted.

Species of the fish genus *Astyanax* Baird & Girard, 1854, are found from the Nueces River, Texas, to Patagonia, Argentina (Bănărescu 1990). This genus is among the most dominant group of freshwater fishes in this extensive region. The number of valid species of *Astyanax* that inhabits Mexico is uncertain (Contreras-Balderas & Lozano-Vilano 1998, Schmitter-Soto 1998). Because of the overall morphological similarity of the species of this genus, there is considerable confusion concerning species distinctness and distribution. Contributing to this problem is the fact that the original descriptions of many of them are incomplete, and data for collection localities were not clearly provided and are often unknown. These problems are reflected in the present nomenclatorial confusion (Valdez-Moreno 1997, Contreras-Balderas & Lozano-Vilano 1998).

Despite these uncertainties, most researchers, including Contreras-Balderas & Lozano-Vilano (1998), agree that one of the valid species is the northern form, *Astyanax mexicanus* (Filippi, 1853). It is known from central Texas, Rio Bravo (named Rio Grande in the U.S.A.), along Gulf of Mexico drainages such as the lower Pánuco River, and through the Tecolutla–Cucharas systems (Miller 1978, Obregón-Barboza et al. 1994, Valdéz-Moreno 1997). However, some authors, such as Espinosa-Pérez et al. (1993), considered forms from the Rio Balsas and the Papaloapan basins extending to Petén, Guatemala, to be *A. mexicanus* s. l. Others (e.g., Paulo Maya 1994), reported the presence of two distinct forms of *Astyanax* in the Río Balsas samples, without selecting names or referring them to either of the two nominal species described from the basin, *Astyanax nitidus* Bocourt (1868) and *A. fulgens* Bocourt (1868).

The identity of the Río Balsas form is still unresolved. We concur with Miller (in litt.) and Contreras-Balderas & Lozano-Vilano (1998) that Mexican forms of *Astyanax* are not the same as the South American representatives assigned to *A.* "*fasciatus*", and none of the Río Balsas forms are *A.*

mexicanus. Such forms probably represent a species of the *A. aeneus* group. Further research is needed to solve this problem.

Many studies of *A. mexicanus* deal primarily with morphometry (Schuppa 1984, Paulo-Maya 1994). Except for minor references to certain bones by Lozano-Vilano & Contreras-Balderas (1990), none deals with osteology. This approach contrasts with other studies in characid fishes. For example, the osteology of the American characid, *Brycon meeki,* was described in detail by Weitzman (1962). Menezes (1969) considered osteology in his study of the phylogeny of the tribe Acestrorhynchini, and Weitzman & Fink (1983) used osteological characters to elucidate relationships among neon tetras, *Paracheirodon* spp. Vari & Harold (1998) diagnosed the genus *Creagrutus* as a monophyletic group within the family Characidae on the basis of some modifications of skull bones. Malabarba (1998) provided a new diagnosis of the Cheirodontinae using features of the dentary, tooth morphology and other skull bones. Vari (1989a) studied the structure of the skull in members of the family Curimatidae and the genus *Pseudocurimata.* Vari (1983) also used osteological information to hypothesize relationships within Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae, as well as relationships among the Ctenoluciidae (Vari 1995). A cladistic analysis based on osteology by Buckup (1998) proposed relationships of the Characidiinae with the Crenuchinae. Langeani (1998) hypothesized the monophyly of the family Hemiodontidae using characteristics of skull bones along with other data.

The posterior region of skull and pectoral girdle of a female *A. mexicanus* from Guayalejo River, Tamaulipas, Mexico, was described and figured by Weitzman & Fink (1983, 1985), but they did not describe the entire skull of this species. The skull anatomy of *A.* "*fasciatus*" has been described only for the form from Balsas River, Mexico, by Mejía-Mójica & Díaz-Pardo (1991). Problems with the identity of this form were discussed above.

The purposes of this work are to describe in detail the skull of *A. mexicanus* and to provide a baseline to compare with other species and genera. The use of the cranial characters described herein may provide a means to better study the taxa assigned to the genus *Astyanax* and could be useful to make inferences about the phylogeny of members of the genus or the family.

Methods

Material examined.—Twenty adult specimens of *Astyanax mexicanus* (>40 mm standard length, SL), from the Fish Collection of the Autonomous University of Nuevo León (UANL), were selected from Rio Grande/Río Bravo localities: Río Salado at Socavón, 5.2 km SW from Múzquiz, State of Coahuila (UANL-7271: 3 ♀ and 2 ♂ SL = 57.47 to 74.67 mm); Rio Conchos: Río Chuvíscar at Aldama, State of Chihuahua (UANL-6944; 4 ♀ and 1 ♂ SL = 46.69 to 54.74 mm); Río Alamo in Paso de las Anacuas, 26 km W from Ciudad Mier, State of Tamaulipas (UANL-3932; 3 ♀ and 2 ♂ SL = 53.71 to 60.11 mm), and Río San Juan: Cañón de la Boca, 1 km after the dam Presa de la Boca, State of Nuevo León (UANL-4924; 5 ♀ SL = 67.65–75.54 mm).

The specimens were cleared and stained following the technique of Hollister (1934). Terminology follows Weitzman (1962),

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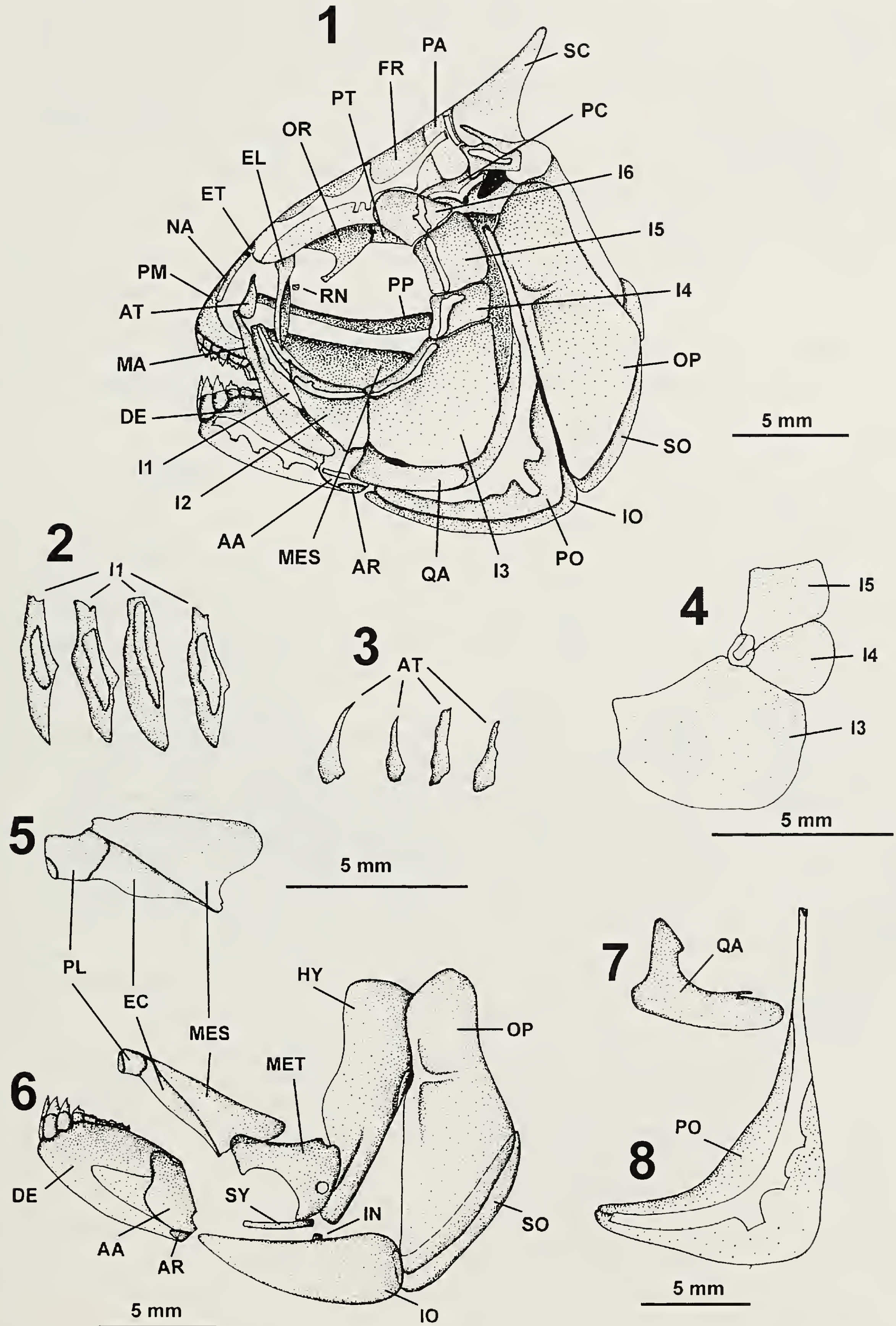
Figs. 1–8. Skull of *Astyanax mexicanus,* lateral view, left side, female, SL 74.29 mm. 1, Full view; 2, Infraorbital I, different shapes; 3, Antorbital, different shapes; 4 Infraorbital 4, malformation; 5, Palatine, ectopterygoid and mesopterygoid; 6, Lower jaw, opercular series, mandibular arch and palatine arch; 7, Quadrate; 8, Preopercular. Abbreviations.—AA—anguloarticular; AT—antorbital; AR—retroarticular; DE—dentary; EC—



ctopterygoid; EL—lateral ethmoid; ET—ethmoid; FR—frontal; HY—hyomandibular; I1—infraorbital 1; I2—infraorbital 2; I3—infraorbital 3; I4—infraorbital 4; I5—infraorbital 5; I6—infraorbital 6; IN—interhyal; IO—interopercle; MA—maxilla; MES—mesopterygoid; MET—metapterygoid; NA—nasal; OP—opercle; OR—orbitosphenoid; PA—parietal; PC—pterotic; PL—palatine; PM—premaxilla; PO—preopercle; PP—parasphenoid; PT—pterosphenoid; QA—quadrate; RN—rhinosphenoid; SC—supraoccipital; SO—subopercle; SY—symplectic.

Fink & Fink (1981) and Weitzman & Fink (1983). Each bone was drawn with the aid of a camera lucida attached to a stereomicroscope (Nikon SMZ10). All base drawings of the bones for *A. mexicanus* were made from specimens collected in the Rio Salado, Coahuila. Morphological differences and similarities between populations were analyzed by direct comparison of shape.

Description of the skull of *Astyanax mexicanus* (Filippi, 1853)

Diagnosis.—Skull circular in lateral profile. Anterior margin of dentary never projecting anteriorly further than that of premaxilla. Opercle almost rectangular. Infraorbital 2 triangular, never overlapping inferior margin of infraorbital 3. Infraorbital 3 semicircular, never reaching laterosensory canal of preopercular bone. Supraoccipital short with wider base; in dorsal view, posterior end of supraoccipital spine slighthly overlapping posterolateral border of epioccipital. Palatines, ectopterygoids and mesopterygoids without teeth. First suspensory pharyngeal triangular, without teeth; second one almost rectangular, with few unicuspid teeth; third one triangular, larger than first and second, with numerous unicuspid teeth. Premaxilla with two rows of teeth. Outer row consisting of four tricuspid teeth, inner row with four to five teeth, each tooth with three to six cusps. Maxilla with single row of one or two teeth, number of cusps per tooth five to eight. Dentary with single row of four teeth followed by several posterior ones; first and third teeth similar in size and appearance. All dentary teeth with five to seven, usually six, cusps. Fifth dentary tooth smaller than first four, with five to six cusps, usually five. Remaining five to ten teeth smaller, each bearing one or two cusps. Symphyseal and lateral diastemmas absent. Total number of anterior gill rakers on first arch 18 to 21, second and third arches 18 to 20, and fourth arch 13 to 18. Five posterior gill rakers on first arch, five to six on second, 14 to 16 on third, and five to six on fourth. Dorsal border of lower pharyngeal with six to ten structures similar to gill rakers. All gill rakers conical in shape and with several short conical spicules arranged irregularly.

Cranium

Ethmoid (Figs. 1, 17, 20, 21).—Most anterior medial bone of the cranium; ethmoid relatively flat but complex in shape. Anteriorly bearing a forward-projecting conical bony process rounded towards the anterior end and two wing-like lateral processes. Ethmoid articulating anteriorly with the nonmovable premaxillae, ventrally with the vomer and lateral ethmoids and posteriorly with the frontals.

Lateral ethmoids (Figs. 1, 17, 20, 21).—Paired bones, each articulating dorsally with a frontal and medially with the vomer. Each lateral ethmoid a thin, triangular plate with a foramen. Angle of internal ventral part of each plate projecting posteriorly and bearing a variable number of small processes with smooth surfaces. Lateral ethmoids separating nasal cavity from ocular cavity and thus, in part, forming anterior wall of eye socket.

Vomer (Figs. 17, 21).—Median bone forming part of roof of mouth cavity. Vomer "T" shaped, the lateral processes artic-

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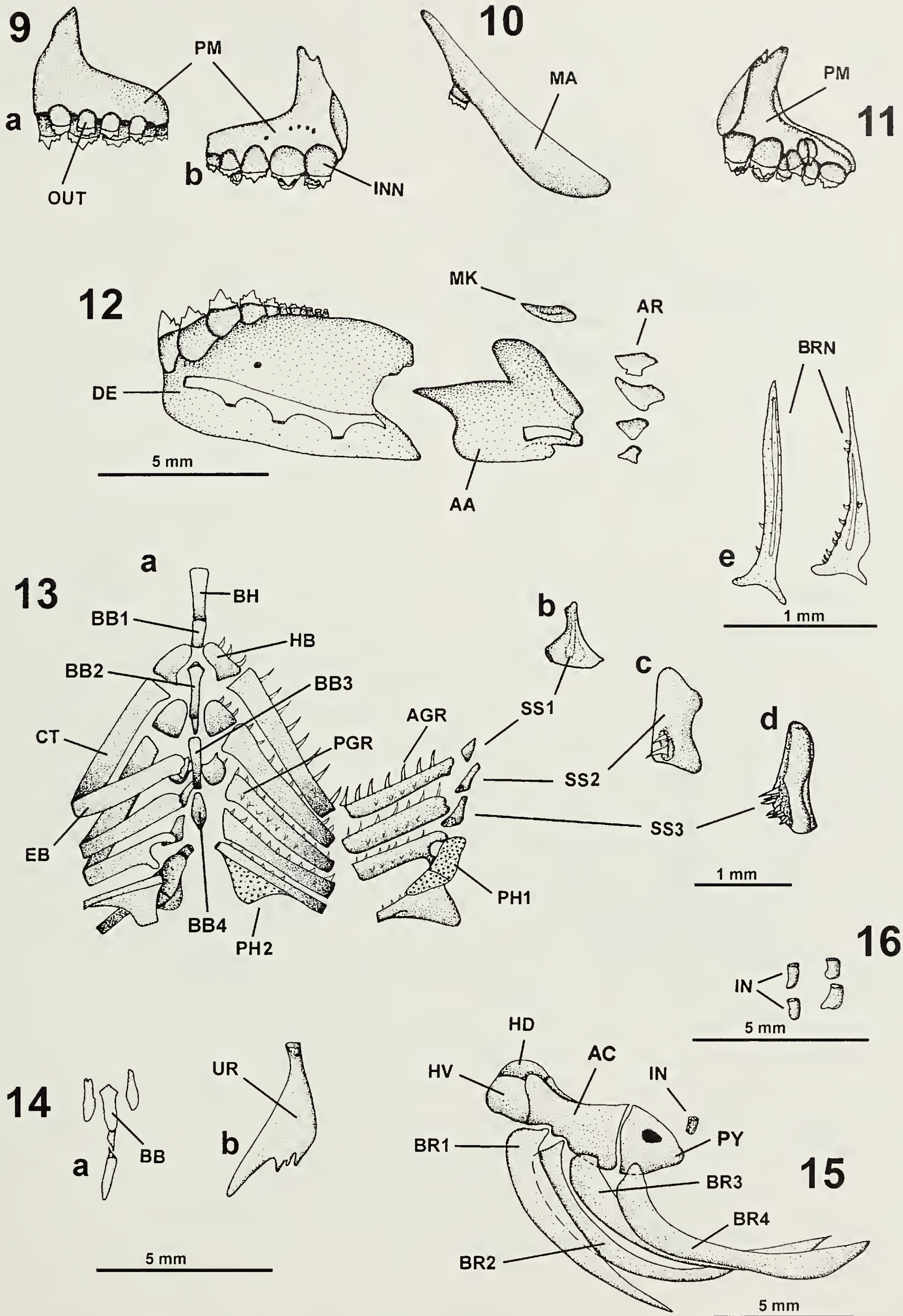
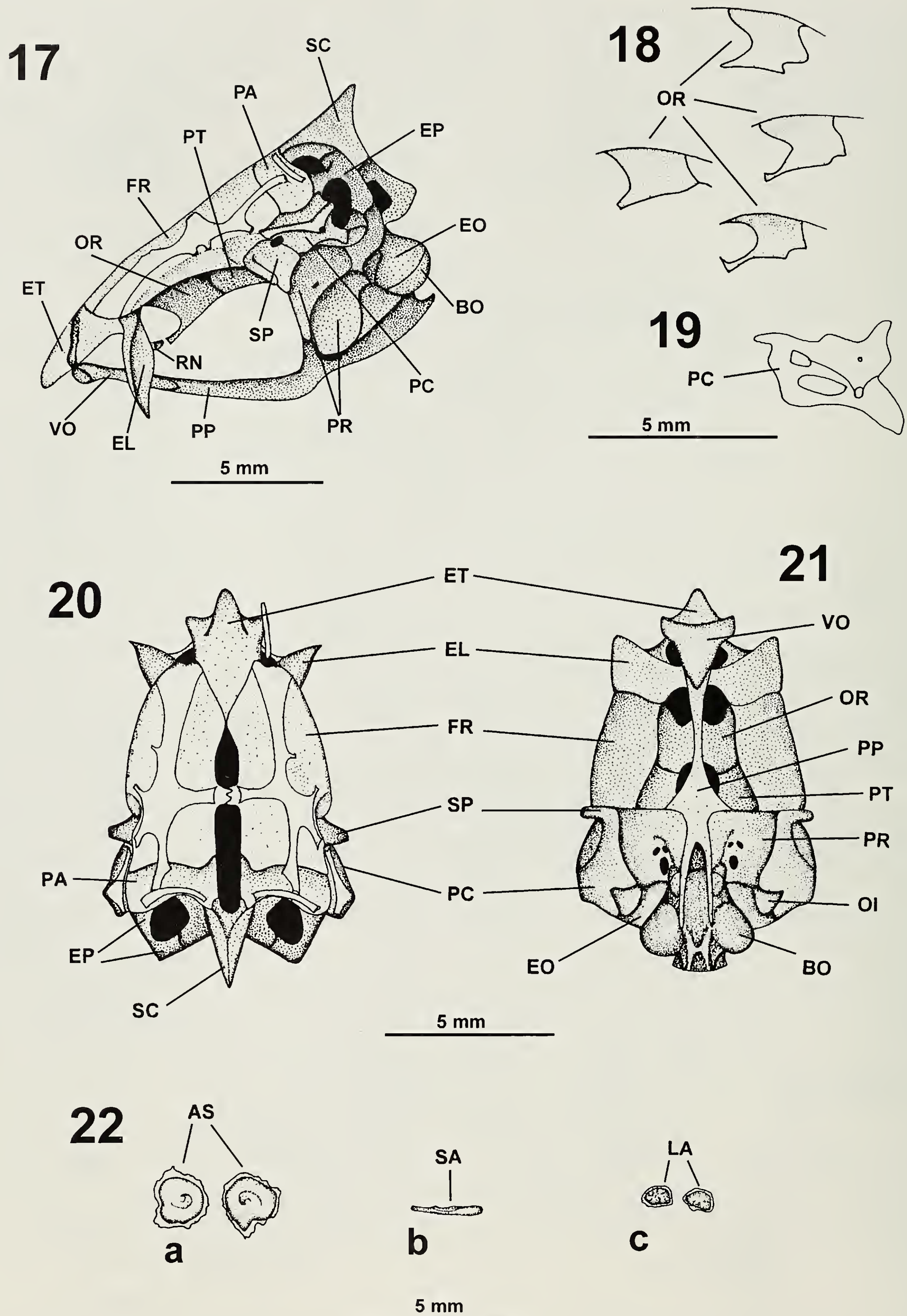
Figs. 9–12. Upper and lower jaws of *A. mexicanus*, female, SL 74.29 mm. 9a, Premaxilla dorsal view; 9b, Premaxilla, ventral view; 10, Maxilla, lateral view; 11, Premaxilla, ventral view, malformation; 12, Dentary, lateral view. Figs. 13, 14a. Branchyal arches of *A. mexicanus*, female, SL 74.29 mm. 13a, Branchyal arches; 13b, suspensory pharyngeal 1; 13c, suspensory pharyngeal 2; 13c, suspensory pharyngeal 3; 13e, gill rakers; 14a, basibranchials malformation. Figs. 14b–16. Hyoid arch of *A. mexicanus*, female, SL 74.29 mm. 14b, Urohyal; 15, Hyoid arch; 16, Interhyal with different shapes. Abbreviations.—AA—anguloarticular; AC—anterior



ceratohyal; AGR—anterior gill rakers; AR—retroarticular; BB1—basibranchials 1; BB2—basibranchials 2; BB3—basibranchials 3; BB4—basibranchials 4; BH—basihyal; BR1—branchiostegal ray 1; BR2—branchiostegal ray 2; BR3—branchiostegal ray 3; BR4—branchiostegal ray 4; CT—ceratobranchials; DE—dentary; EB—epibranchials; HB—Hypobranchials; HD—hypohyal dorsal; HV—hypohyal ventral; IN—interhyal; INN—inner row of teeth; MA—maxillary; MK—meckelian cartilage; OUT—outer row of teeth; PGR—posterior gill rakers; PH1—upper pharyngeal teeth; PH2—lower pharyngeal teeth; PM—premaxilla; PY—posterior ceratohyal; SS1—suspensory pharyngeals 1; SS2—suspensory pharyngeals 2; SS3—suspensory pharyngeals 3; UR—urohyal.



Figs. 17–22. Cranium of *A. mexicanus,* female, SL 74.29 mm. 17, lateral view. 18, Orbitosphenoid, different shapes; 19, Pterosphenoid, different shape; 20, dorsal view; 21, ventral view; 22a, Otolith asteriscus, dorsal view; 22b, Otolith sagitta, dorsolateral view; 22c, Otolith lapillus, dorsal view. Abbreviations.—AS—asteriscus; BO—basioccipital; EL—lateral ethmoid; EO—exoccipital; EP—epioccipital; ET—ethmoid; FR—frontal; LA—lapillus; OI—opisthotic; OR—orbitosphenoid; PA—parietal; PC—pterotic; PP—parasphenoid; PR—prootic; PT—pterosphenoid; RN—rhinosphenoid; SA—sagitta; SC—supraoccipital; SP—sphenotics; VO—vomer.

ulating with the lateral ethmoids. Two foramina providing passages for ramus buccalis of facial nerve. Ventrally, vomer articulating with parasphenoid and dorsally with ethmoid. Ventral surface of vomer without anatomical markings, few present on dorsum.

Frontals (Figs. 1, 17, 20, 21).—Laminar bones comprising a large part of dorsal region of cranium, connected to each other by epiphyseal bar that bridges the cranial fontanels. Each frontal with a ventral keel in medial position. Frontal articulating dorsoposteriorly with parietal, dorsoanteriorly with ethmoid, nasal and lateral ethmoid, and ventrally with orbitosphenoid, pterosphenoid, sphenotics, and pterotic. Each frontal containing canals of accoustico lateralis system. Anterior portions of these canals wide and continuous with nasal canal. Frontal bone with medial canals splitting in two main branches: an epiphysial branch extending medially over the epiphysial bar and opening above the frontal fontanel, and posterior branch connected posteriorly with the parietal and this canal, but not to extrascapular canal. Another branch, smaller than the former two, runs laterally continuing with the pterotic canal. Small side branches of these canals opening on dorsal surface of frontal.

Parietals (Figs. 1, 17, 20).—Rectangular laminar paired bones, without anatomical markings on their ventral and dorsal surfaces. Each one articulating dorsoanteriorly with frontal, posteriorly with epioccipital, dorsoposteriorly with supraoccipital and lateroventrally with pterotic. Parietals separated by the cranial fontanel. Laterosensory canal parietal connecting posterolaterally with extrascapular canal and extending dorsally to cranial fontanel.

Supraoccipital (Figs. 1, 17, 20).—Median bone constituting posterior roof of cranium, articulating dorsoanteriorly with parietals and forming posterior border of median dorsal fontanel, ventrolaterally with epioccipitals, and ventrally with pterotics. In dorsal view, supraoccipital "V" shaped, with a wide anterior base. Dorsal surface with a groove extending posteriorly to end of supraoccipital spine.

Epioccipitals (Figs. 17, 20).—Smooth tubular paired bones, each containing a major portion of the posterior vertical semicircular canal of the auditory and equilibrium systems. Epioccipital articulating dorsally with supraoccipital, posteroventrally with exoccipital and anteroventrally with pterotic. Lateral epioccipital process anteriorly contacting parietal and pterotic, dividing postemporal fossa in two parts.

Exoccipitals (Figs. 17, 21).—Smooth paired bones forming ventral part of posterior cranium, dorsally articulating with epioccipital, ventrally with basioccipital, anteriorly with prootic and anterolaterally with pterotic and opisthotic. Each exoccipital with laminar part enclosing the foramen magnum and ventral spherical part constituting the roof of the otic capsule for lagena.

Opisthotics (Fig. 21).—Small, thin bones, having triangular shape with a curved base, located external to articulation between pterotic, exoccipital and prootic; opisthotic attaching by ligament to ventral process of postemporal bone.

Basioccipital (Figs. 17, 21).—Constituting posterior base of cranium, with one globular part and other laminar. Dorsally articulating with exoccipitals, anteriorly with prootic, ventromedially with parasphenoid and posteriorly with first vertebra. Basioccipital also forming ventral portion of otic capsule for lagena and posterior region of saccular cavity for asteriscus. No anatomical markings on external surface.

Pterotics (Figs. 17, 20, 21).—Paired bones articulating anteriorly with sphenotic, ventromedially with prootic, dorsally with frontal and parietal, and posteriorly with epioccipital. Pterotic with rounded process that projects posteriorly and ventrally, providing insertion for levator operculi muscle. Pterotic articulating with hyomandibular at a groove. Internally, pterotic enclosing a major part of the horizontal semicircular ca-

nal. Each pterotic with a "V"-shaped canal of the accoustico lateralis system, canal continuing ventrally to preopercular canal and dorsally to frontal canal. A small foramen present between pterotic and sphenotic. Extrascapular overlapping posterodorsal part of pterotic.

Sphenotics (Figs. 17, 20 21).—Paired bones, quadrangular with rounded edges in lateral view and with a strong rounded process anterodorsally. Sphenotics articulating anteriorly with pterosphenoid, ventrally with prootic, posteriorly with pterotic and dorsally with frontal. Sphenotic not associated with lateral sensory system.

Prootics (Figs. 17, 21).—Complex paired bones. Dorsolaterally articulating with sphenotics and pterotics, medially with prootic on the other side, anteriorly with pterosphenoid, ventrally with parasphenoid, and posteriorly with opisthotic, exoccipital and basioccipital. Prootic with three foramina of different sizes, the auditory foramen largest.

Parasphenoid (Figs. 1, 17, 21).—Longest unpaired bone of cranium, spanning ventral median region of cranium and articulating anteriorly with vomer, dorsoposteriorly with prootics and basioccipitals. Ventrally with a medial quilla joining with suspensor pharyngeals by ligaments. Ventroposteriorly ending in two laminar process.

Pterosphenoids (Figs. 1, 17, 21).—Paired bones, rectangular in lateral view, with smooth edges, forming part of wall and floor of cranial cavity. Together with orbitosphenoid, pterosphenoids constituting medial aspect of ocular cavity. Pterosphenoid articulating dorsally with frontal, laterally with sphenotic, ventrally with parasphenoid, and anteriorly with orbitosphenoid. A small foramen for trochlear nerve present at articulation of orbitosphenoid and pterosphenoid.

Orbitosphenoid (Figs. 1, 17, 21).—Located ventral to middle region of frontal and posterior to ethmoid. Anterodorsally articulating with frontal and posteriorly with pterosphenoid. Ventrally, orbitosphenoid with a process directed toward anterior part of cranium. Orbitosphenoid highly varible in shape, length, and width at intra- and interpopulation levels (Fig. 18), usually resembling a "J" in lateral view. In dorsal view, orbitosphenoid resembling two wings or a "bird in flight" (Mejía-Mojica & Díaz-Pardo 1991).

Rhinosphenoid (Figs. 1, 17).—Small, almost square to irregular medial bone located anteriorly to orbitosphenoid, between lateral ethmoids. Rhinosphenoid ossified in five of our specimens.

Nasals (Fig. 1).—Tubular paired bones, slightly curved with smooth surface, located anterolateral to cranium. Nasal articulating anteriorly with premaxilla, posteriorly with frontal. Each nasal bone containing a branch of the laterosensory system.

Otoliths (Fig. 22a, b, c).—The ovoid lapillus contained in an utricular sac on floor of prootic. The spine-like sagitta contained in saccular recess formed by prootic, basioccipital and exoccipital. The lenticular asteriscus lying in capsule formed by the exoccipital and basioccipital. Asteriscus larger than the other otoliths and bearing small projections around its border.

Antorbital and Infraorbital bones.—This series comprising seven paired elements as follows:

Antorbitals (Fig. 1).—Each bone located ventrolaterally to respective nasal orifice. Antorbital with an elongated triangular shape, the anterior part considerably narrower than the posterior part; however, shape of antorbital varying among specimens. This variation apparently independent of sex (Fig. 3).

Infraorbitals 1 (Figs. 1, 2).—Shape similar to the blade of a scalpel, the ventral border variably prolonged in width and length. First infraorbital partially overlapped by the maxilla.

Infraorbitals 2 (Fig. 1).—Triangular bone with inferior margin usually smooth or sometimes jagged. Posterior portion of bone deeper than anterior portion. Second infraorbital located lateral to anguloarticular

and quadrate bones and never overlapping inferior margin of infraorbital 3.

Infraorbitals 3 (Figs. 1, 4).—Largest bone of the series. Shape semicircular. Inferior margin always smooth, lateral surface occasionally with small foramina. Third infraorbital located lateral to quadrate and preopercle, but inferior margin never reaching laterosensory canal of preopercular bone.

Infraorbitals 4 (Figs. 1, 4).—Rectangular bone, shape depending on shape of articulation with infraorbital 3. Anteroventral edge projecting ventrally. Fourth infraorbital located lateral to hyomandibular bone.

Infraorbitals 5 (Figs. 1, 4).—Quadrangular bone with rounded corners. Located dorsal to infraorbital 4 and lateral to hyomandibular.

Infraorbital 6 (Fig. 1).—Thumb-nail shaped bone, posteroventral margin roughly straight at articulation with fifth infraorbital. Sixth infraorbital located lateral to sphenotic and frontal.

All the circumorbital bones smooth and bearing canals for the accoustico lateralis system. Canal of sixth infraorbital connecting with laterosensory canals of pterotic and frontal bones. *Astyanax mexicanus* lacking supraorbital bones.

Upper Jaw

Premaxillae (Figs. 1, 9).—Strong, paired bones articulating dorsally with ethmoid and nasal bones, laterally with maxillae. Premaxilla triangular in dorsal view. Each premaxilla with two teeth rows. In one specimen a replacement row present. Anterior row consisting of four teeth, each one having three, sometimes four, cusps. Posterior row with four to five teeth, each one with three to six cusps. Dorsal surface of premaxilla smooth, ventral surface with a small foramen. One specimen with a tooth malformation in the posterior row (Fig. 11).

Maxillae (Figs. 1, 10).—Thin, paired bones, each articulating anteriorly with premaxilla. Posterior ramus of maxilla overlapping dentary and bearing one or two teeth, each with five to eight cuspids.

Lower Jaw

Dentaries (Figs. 1, 6, 12).—Paired robust bones, each articulating dorsoposteriorly with anguloarticular and retroarticular, posteromedially with coromeckelian bone. Dentary with a single row of four frontal teeth and several posterior ones. First and third frontal teeth similar in size and appearance; second one about the same size or slightly smaller than the first. The fourth smaller than the other three frontal teeth. All of them with five to seven, usually six, cusps. Fifth dentary tooth smaller than the first four, with five or six cusps, usually five. Remaining teeth smaller (five to ten), with one or two cusps. Replacement row of teeth always present but variously developed and positioned, teeth of replacement row directed vertically.

Lateral surface of each dentary with a canal for accoustico lateralis system, associated with three small foramina. Posterior portion of this canal continuous with the anguloarticular canal. Symphyseal and lateral diastemmas absent.

Anguloarticulars (Figs. 1, 6, 12).—Paired bones that form the joint between the dentary and skull, shape similar to a fan with three peaks, middle one longest and pointed, other two rounded. Anguloarticular articulating anteriorly with dentary, ventroposteriorly with retroarticular, posteriorly with quadrate via a condyle, and medially with Coromeckelian bone. Anguloarticular containing a canal of the lateral sensory system that communicates posteriorly with canal of preopercle.

Retroarticulars (Figs. 1, 6, 12).—Paired, triangular bones, equal to or slightly smaller than coromeckelian bone. Retroarticular articulating ventroposteriorly with anguloarticular. Shape and length of retroarticular variable.

Coromeckelian bones (Fig. 12).—Small, paired, oval bones with smooth external

surface, located along medial face of anguloarticular. Medial surface of coromeckelian with a median keel.

Opercular Series

Opercles (Figs. 1, 6).—Thin, paired, nearly rectangular bones with smooth surfaces and borders. Opercle articulating anteriorly with hyomandibular via a condyle on the latter, opercle articulating ventrally with subopercle.

Subopercles (Figs. 1, 6).—Thin, paired bones with smooth surfaces and borders articulating dorsally with opercle. Anterior part of subopercle with a small dorsal process.

Interopercles (Figs. 1, 6).—Paired, flat, smooth bones with triangular shape, posterior portion deeper than anterior part. Interopercle articulating dorsally with preopercle.

Preopercles (Figs. 1, 8).—Large, flat, paired bones, the dorsal limb lying between hyomandibular and opercle. Preopercle roughly triangular in shape, with a broad base and thin dorsal limb. A canal of the laterosensory system extending the length of preopercle; anteriorly, the canal continuous with anguloarticular canal, dorsally the canal continuous with pterotic canal.

Mandibular Arch

Hyomandibulars (Fig. 6).—Strong, paired bones with smooth surfaces. Dorsal portion of bone broad with rounded margins, ventral part slender. Hyomandibular articulating dorsally with neurocranium through a fossa in the pterotic and another in the sphenotic. Dorsoposteriorly, hyomandibular articulating with opercle, ventrally with metapterygoid.

Quadrates (Figs. 1, 7).—Paired bones lying above preopercle and articulating anteroventrally with anguloarticular by a condyle. Quadrate L-shaped, with vertical limb shorter than horizontal one. A posteriorly directed process of varying size sometimes present along dorsal margin of horizontal limb. Variation in this process apparently independent of sex.

Symplectics (Fig. 6).—Two smooth rodlike bones, slightly curved or straight, located medial to quadrate bone.

Palatine Arch

Metapterygoids, mesopterygoids, ectopterygoids, palatines and the vertical part of quadrate forming the anterior suspensory mechanism of lower jaw.

Metapterygoids (Fig. 6).—Paired bones of irregular shape with smooth surfaces. A small foramen present on posterior portion of metapterygoid. Posterior portion of bone deeper than anterior part. Two processes of variable size present on dorsal surface of posterior portion of metapterygoid. Metapterygoid articulating dorsoanteriorly with mesopterygoid and dorsoposteriorly with hyomandibular.

Mesopterygoids (Figs. 5, 6).—Paired triangular bones with smooth surfaces. Mesopterygoid articulating anteriorly with palatine, anteroventrally with ectopterygoid, and ventrally with metapterygoid and quadrate.

Ectopterygoids (Figs. 5, 6).—Paired triangular bones adjacent to mesopterygoids. Ectopterygoid narrower than mesopterygoid but of similar surface morphology and thickness.

Palatines (Figs. 5, 6).—Paired bones, square shaped with slightly rounded angles. Palatines articulating anteriorly with maxillary and posteriorly with ectopterygoids and mesopterygoids.

Mesopterygoid, ectopterygoid and palatine bones without teeth.

Hyoid Arch

Interhyals (Figs. 6, 15, 16).—Small, cylindrical, paired bones, lying ventral to hyomandibular and posterior to symplectic. Interhyal located below interopercle, articulating with hyomandibular and symplectic.

Posterior ceratohyals (Fig. 15).—Paired triangular bones with rounded posterior end

and smooth borders and surfaces. A foramen located centrally or somewhat closer to the posterior border, associated or not with a canal. Posterior ceratohyal articulating anteriorly with anterior ceratohyal and posteriorly with interhyal. Ventrally posterior ceratohyal supporting fourth branchiostegal.

Anterior ceratohyals (Fig. 15).—Paired bones, rectangular in lateral view, with smooth surfaces. Anterior ceratohyal articulating anteriorly with dorsal and ventral hypohyals, posteriorly with posterior ceratohyal, and, ventrally, supporting first three branchiostegal rays. Third branchiostegal ray overlying and articulating with most posteroventral part of anterior ceratohyal. First and second branchiostegal rays inserted into small grooves on ventral margin of anterior ceratohyal.

Dorsal hypohyals (Fig. 15).—Shallow paired bones overlying and articulating with ventral hypohyal and anterior ceratohyal.

Ventral hypohyals (Fig. 15).—Paired quadrangular bones with rounded angles, articulating with anterior ceratohyals and dorsal hypohyals.

Urohyal (Fig. 14b)—Triangular bone bearing projections on the ventral surface of varying length and number. Urohyal inserting between and connected by ligaments to ventral hypohyals.

Branchial Arches

Basihyal (Fig. 13a).—This rectangular and slightly flattened median bone the anteriormost element of the branchial skeleton. Basihyal located between dorsal hypohyals. In one specimen, first basibranchial malformed (see Fig. 14a).

Basibranchials (Fig. 13a).—Together with the basihyal, these four unpaired bones forming the median spine of the gill-arch skeleton. Anteriormost basibranchial flattened and attached by a ligament to basihyal; second and third basibranchials elongated; and fourth leaf-shaped and smaller than preceding two. A shared basibranchial cartilage uniting all basibranchials.

Hypobranchials (Fig. 13a).—Three paired bones comprising most proximal elements of first three gill arches. First hypobranchial tongue-shaped, articulating with first basibranchial and first ceratobranchial. Second hypobranchial dome-shaped, articulating with second basibranchial and second ceratobranchial. Third hypobranchial saccular-shaped, articulating with third basibranchial and third ceratobranchial. All hypobranchials bearing gill rakers on anterior edge.

Ceratobranchials (Fig. 13a).—Five paired bones that form most of the ventral part of each gill arch. First three ceratobranchials elongated and slightly flattened, each articulating proximally with a hypobranchial and distally with an epibranchial. Fourth ceratobranchial elongated and slightly flattened, articulating proximally with a hypobranchial and distally with fourth epibranchial. First four ceratobranchials bearing gill rakers along anterior and posterior edges. Fifth ceratobranchial modified to form lower pharyngeal bone, which bears several small, scattered, unicuspid teeth on its dorsal surface and gill rakers along the anterior edge.

Epibranchials (Fig. 13a).—Four paired bones forming most of dorsal portion of each gill arch. First two elongated, slightly flattened, and lacking uncinate processes. Third elongated and bearing posteriorly directed uncinate process near distal end of bone; uncinate process articulating with upper pharyngeal teeth. Fourth epibranchial triangular. All epibranchials with small rakers along anterior edge, and first three with gill rakers along posterior edge.

Third and fourth epibranchials supporting upper pharyngeal plate. Upper pharyngeal irregular in shape and with several small, scattered unicuspid teeth on ventral surface.

Suspensory pharyngeals.—Three small, paired bones articulating with first three epibranchials and with parasphenoid. First

one triangular, without teeth (Fig. 13b). Second almost rectangular with few unicuspid teeth (Fig. 13c). Third triangular with numerous unicuspid teeth (Fig. 13c).

Gill Rakers.—Total number of anterior gill rakers on first arch 18 to 21, second and third arches 18 to 20, and fourth arch 13 to 18. Five posterior gill rakers on first arch, five to six on second, 14 to 16 on third, and five to six on fourth. Dorsal border of lower pharyngeal with six to ten structures similar to gill rakers. All gill rakers conical in shape and with several short conical spicules arranged irregularly.

Discussion

The skull of *Astyanax mexicanus* is made up of 58 bones, nine of them unpaired (ethmoid, vomer, parasphenoid, supraoccipital, orbitosphenoid, basioccipital, urohyal, basihyal, rhinosphenoid), all others are paired. This number differs from that reported for *Astyanax* "*fasciatus*" (sensu Mejía-Mojica & Díaz-Pardo 1991), because they did not include the rhinosphenoid.

A comparison of the skull between *A. mexicanus* and the descriptions of *A.* "*fasciatus*" sensu Mejía-Mojica & Díaz-Pardo 1991, suggests that they are quite similar. However, differences are present in some bones. The opercle in *A. mexicanus* is almost rectangular and wide, whereas in *A.* "*fasciatus*" it is more rhomboid-like and narrower. The supraoccipital (in dorsal view) is short with a wide base in *A. mexicanus,* whereas in *A.* "*fasciatus*" it is longer with a narrow base. Infraorbital 3 in *A. mexicanus* is semicircular, in in *A.* "*fasciatus*" it is angular. Infraorbital 2 has a wide margin articulating with infraorbital 3 in *A. mexicanus,* whereas this margin is narrower in *A.* "*fasciatus.*"

Also, Mejía-Mojica & Díaz-Pardo (1991) described the posterior ceratohyal in *A.* "*fasciatus*" as having a foramen associated with a canal, whereas in *A. mexicanus* it may or may not be associated with a canal. The number of teeth cusps reported from the mandibular bones are different among the two species. All teeth are pentacuspid in *A.* "*fasciatus*," whereas in *A. mexicanus* there are 3–4 cusps on teeth in the outer row, 3–6 cusps on teeth of the inner row of the premaxilla, 5–8 cusps on maxillary teeth, and 2–6 on dentary teeth. Finally, the number of gill rakers varies among the two species: in *A. mexicanus* 11 gill rakers are present on the first arch, whereas in *A.* "*fasciatus*" there are 13. The latter count is similar to that of *A. aeneus,* which has 12–14 gill rakers (Schmitter-Soto 1997).

Mejía-Mojica & Díaz-Pardo (1991) described as unique for *A.* "*fasciatus*" the presence of a small plate with teeth on the third suspensory pharyngeal; however, it is not exclusive to this species. We found this plate in almost all populations of *A. mexicanus* studied. Here we provide the first report of teeth on the second suspensory pharyngeal for *A. mexicanus.*

Most other osteological elements of *A. mexicanus* are very similar to those described for *Astyanax* "*fasciatus*" and are not discussed further. In general, osteology of *A.* "*fasciatus*" of Mejía-Mojica and Díaz-Pardo (1991) resembles that of other southern forms previously described by Valdéz-Moreno (1997), e.g., infraorbital 2 with a short base, infraorbital 3 with a dorso-posterior projection and angulate shape, and supraoccipital long (in dorsal view) with a narrow base. Southern forms studied by Valdéz-Moreno (1997) appear to be *A. aeneus,* based on the work of Lozano and Contreras (1991).

The main osteological difference found between the skull of *A. mexicanus* and *Brycon meeki,* a well-described "representative of characid osteology" (Weitzman 1962), is the presence of supraorbital bones in the latter. The possible significance of the presence or absence of the supraorbital in characid fishes was discussed by Weitzman & Malabarba (1998). The shapes of the infraorbitals, antorbital, quadrate and anguloarticular are different in *A. mexicanus* and *B. meeki.* The rhinosphenoid is larger in *B.*

meeki than in *A. mexicanus*. There are three rows of teeth on the premaxilla in *B. meeki*, two in *A. mexicanus*. There are 13–15 teeth on the maxilla is 13 to 15 in *B. meeki*, one or two in *A. mexicanus*. The pterotic process and sphenotic are longer in *B. meeki* than in *A. mexicanus*. The distribution of teeth on the superior pharyngeal (in five rows in *B. meeki*) is not the same in *Astyanax* (irregular). The canals of the accoustico lateralis system in *A. mexicanus* are similar to those of *Brycon meeki*, except the anterior portion of the canal in the frontal bone in the former is wider. *B. meeki* has more anterior gill rakers (31 to 33) than *A. mexicanus* (18 to 21). Finally, *A. mexicanus* has teeth on suspensory pharyngeals 2 and 3 whereas *B. meeki* does not.

A comparison of *A. mexicanus* with other tetragonopterinae, like *Paracheirodon axelrodi* (Schulz, 1956), reveals even more differences: *P. axelrodi* lacks infraorbitals 4, 5 and 6, and major structural differences are evident in infraorbitals 1 and 2, the pterotic, opercle, hyomandibular, sphenotic, rinosphenoid, and orbitosphenoid (Weitzman & Fink 1983).

The figures of the posterior region of skull and pectoral girdle of female *Astyanax mexicanus*, that appeared with no explanations in Weitzman & Fink (1983), are consistent with our observations.

The presence of two rows of teeth on the premaxillae in our specimens agrees with previous reports for the genus by Eigenmann (1921), Géry (1977) and Mejía-Mojica & Díaz-Pardo (1991). We found the number of maxillary teeth to be only one or two; this agrees with data of Eigenmann (1921), Géry (1977) and Mejía-Mojica & Díaz-Pardo (1991) and is within the range (zero to three) given by Contreras & Rivera (1985) for Mexican forms. The last authors followed Gery (1977) in reporting up to seven maxillary teeth for Central American forms. None of the above citations referred specifically to *A. mexicanus*. Alvarez del Villar (1970) considered the maxillary teeth smooth ("no aserrados", sic), and Contreras-Balderas & Rivera (1985) reported teeth tricuspidate for the genus *Astyanax*; we found these teeth with five to eight cusps in *A. mexicanus*.

The number of dentary teeth in our specimens is the same as that reported by Géry (1977). Alvarez (1970) and Mejía & Díaz-Pardo (1991) mentioned that dentary teeth are pentacuspid in *Astyanax*, whereas Contreras & Rivera (1985) indicated that they are tricuspid for the genus. Apparently, number of cusps is variable in this genus, and may be subject to abrasion, so this character should be considered with caution.

Malformations in the premaxillae (Fig. 12) and the fourth infraorbitals (Fig. 5) were detected in two specimens from Río Salado and Río Alamo. Cailliet et al. (1986) described deformations on the jaws and head of other species of fish, related to heredity and/or enviromental factors. However, this is the first time that malformations are reported for *Astyanax*, and the causes were not addressed in this study.

Acknowledgments

J. J. Schmitter-Soto, and M. Elías-Gutiérrez made valuable comments to the original manuscript. This study is part of a grant given to M. E. Valdéz-Moreno by Conacyt (Number 138485). Lourdes Lozano-Vilano allowed the use of material from the Fish Collection at Universidad Autónoma de Nuevo León, Monterrey, México. H. Mejía-Mójica kindly allowed examination of stained and cleared material from Balsas basin.

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